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THE RELEASE OF THE PEDAL DISK IN AN UNDESCRIBED SPECIES OF *TEALIA* (ANTHOZOA: ACTINIARIA)

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Abstract

Specimens presumed to belong to an undescribed species of *Tealia* were collected subtidally in the northeast Pacific. In contact with the asteroids *Dermasterias imbricata* and *Patiria miniata*, these animals expanded their oral disks, constricted their columns, and detached their pedal disks. Other asteroids had no such effect. Of five other species of *Tealia*, only *T. piscivora* showed similar behavior and only to *D. imbricata.* Electrophysiological records showed: 1) that *D. imbricata* evokes pulses in a slow conduction system (McFarlane's SS1); and 2) that a train of electrical stimuli also causes SS1 pulses and brings about the release. It is concluded that SS1 pulses trigger the releasing behavior of *Tealia* sp. as they do the release and swimming behavior of *Stomphia* spp. A review of pedal disk release in the actinians shows that it occurs only in certain genera and species in several families not closely related. Although the circumstances and functions of the release where known are not the same in different species, the neurophysiological mechanisms employed are strikingly similar. Also discussed are the active role of the pedal disk in special behavior patterns and a possible function of the release in the escape of *Tealia* sp. from a predator.

Introduction

Sea anemones with adhesive pedal disks generally remain firmly fixed to the substratum. If they change positions at all they do so by extremely slow sliding steps across the surface. However, a few anemones detach their pedal disks rapidly in response to specific stimuli. *Calliactis parasitica* (Couch) does so in its symbiotic interactions with hermit crabs (Ross, 1967, 1974), and *Stomphia coccinea* (Müller) and *S. didemon* Siebert (Siebert, 1973) also do so when they encounter certain asteroids and aeolids, moving away afterwards by repeated flexions of the body (Yentsch and Pierce, 1955; Sund, 1958; Robson, 1961). These activities have provided opportunities for studying the behavioral physiology of actinians in general and have contributed to the discovery of the conduction systems that control behavior in these animals (McFarlane, 1969a,b; Lawn, 1976).

The present study began with the observation that specimens believed to belong to *Tealia crassicornis* released their pedal disks when they came into contact with the leatherstar, *Dermasterias imbricata.* Attempts to confirm this gave variable results, a difficulty that was only removed later when Sebens and Laakso (1977) showed that some anemones previously assigned to *T. crassicornis* ranked as a separate species which they named *T. piscivora.* When we tested both species separately we found that specimens of *T. crassicornis* never released their pedal

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disks in response to *D. imbricata* whereas specimens of *T. piscivora* usually did so. About the same time specimens of an undescribed north Pacific *Tealia* were collected which gave an even more striking releasing response to *D. imbricata*. The behavioral physiology of this animal is the subject of this paper. Pending a full systematic description we shall name it *Tealia* sp. A laboratory and subtidal study is now in progress on the behavior and general ecology of *T. piscivora*. This will be the subject of a separate paper.

Materials and Methods

Tealia sp. was collected in Barkley Sound, British Columbia, at depths of 75–110 m. Exact locations and depths are not known because all 8 specimens obtained during 1978–80 came up on separate occasions in a fisherman's net. Another specimen was found in the display tank at the Friday Harbor Laboratory in 1981, but the site and time of its collection are not known. We present here a few features of the 8 animals in our collections: diameter of the tentacular crown, 5–20 cm, and of the pedal disk, 3–14 cm; height of column 4–20 cm; color of column, translucent, grading through pale mauve to pink below the margin; tiny beadlike verrucae on the column in irregular horizontal rows. The animal was judged to be a species of *Tealia* from the decamerous arrangement of the innermost ring of tentacles, the presence of a fosse, the long stout tentacles, and the presence of verrucae resembling those of some other species of *Tealia*. It did not correspond to any known species of *Tealia* as described by Stephenson (1935), Carlgren (1949), and Hand (1955). With so few animals available, priority was given to behavioral and physiological work on the living anemones before preserving specimens for identification.

The animals were kept in aquaria at the Bamfield Marine Station and were fed about once per week on pieces of fish or mollusks. *D. imbricata* and other asteroids were presented to individual anemones and their responses noted and timed. Typical responses were recorded in still and motion pictures for further study.

Electrophysiological techniques followed the standard procedure developed for sea anemones (McFarlane, 1969a,b; Lawn, 1976, 1980). A polyethylene suction electrode was attached to a tentacle for recording purposes, and a similar stimulating electrode was attached to the column.

Results

Behavioral observations

The behavior of *Tealia* sp. and five described species of *Tealia* (*T. coriacea, T. crassicornis, T. lofotensis, T. columbiana, T. piscivora*) was first studied in 10 presentation trials with *Dermasterias imbricata*. The sea stars were brought into contact with firmly attached anemones and kept in contact for 3 min or until the anemone detached its pedal disk. *Tealia* sp. released its pedal disk in 9 and *T. piscivora* in 8 of the 10 trials. None of the other species ever responded in this way. The tentacles of species that did not release normally clung strongly to the sea star as to food, whereas *Tealia* sp. and *T. piscivora* remained in contact without clinging.

Specimens of 14 other asteroids were available at Bamfield for trials with *Tealia* sp. similar to those described above with *Dermasterias*. Only one of these species, *Patiria miniata*, caused frequent release of the pedal disk, 7 times in 20 trials. Two other species caused the pedal disk to release occasionally: *Solaster stimpsoni* once in 20 trials; *Crossaster papposus* once in 14 trials. The following 11 species, each tested 20 times, never caused the pedal disk to release: *Evasterias troscheli, Henricia leviscula, Hippasteria spinosa, Leptasterias hexactis, Mediaster aequalis, Orthasterias koehleri, Pisaster brevispinus, Pisaster ochraceus, Pteraster tesselatus, Pycnopodia helianthoides, and Solaster dawsoni.*

Release times provided further evidence that *Dermasterias* (mean time 33 sec in 14 releases) was considerably more effective than *Patiria* (mean time 78 sec in 7 releases). The single releases to *Crossaster papposus* and *Solaster stimpsoni* took place at 130 and 180 sec, respectively. These results suggest that the release is triggered by substances which are present and deliverable in amounts that can cause release frequently in only two of the asteroids tested. Possibly these substances occur in other asteroids also but only at levels that are usually below the threshold that causes the release of the pedal disk.

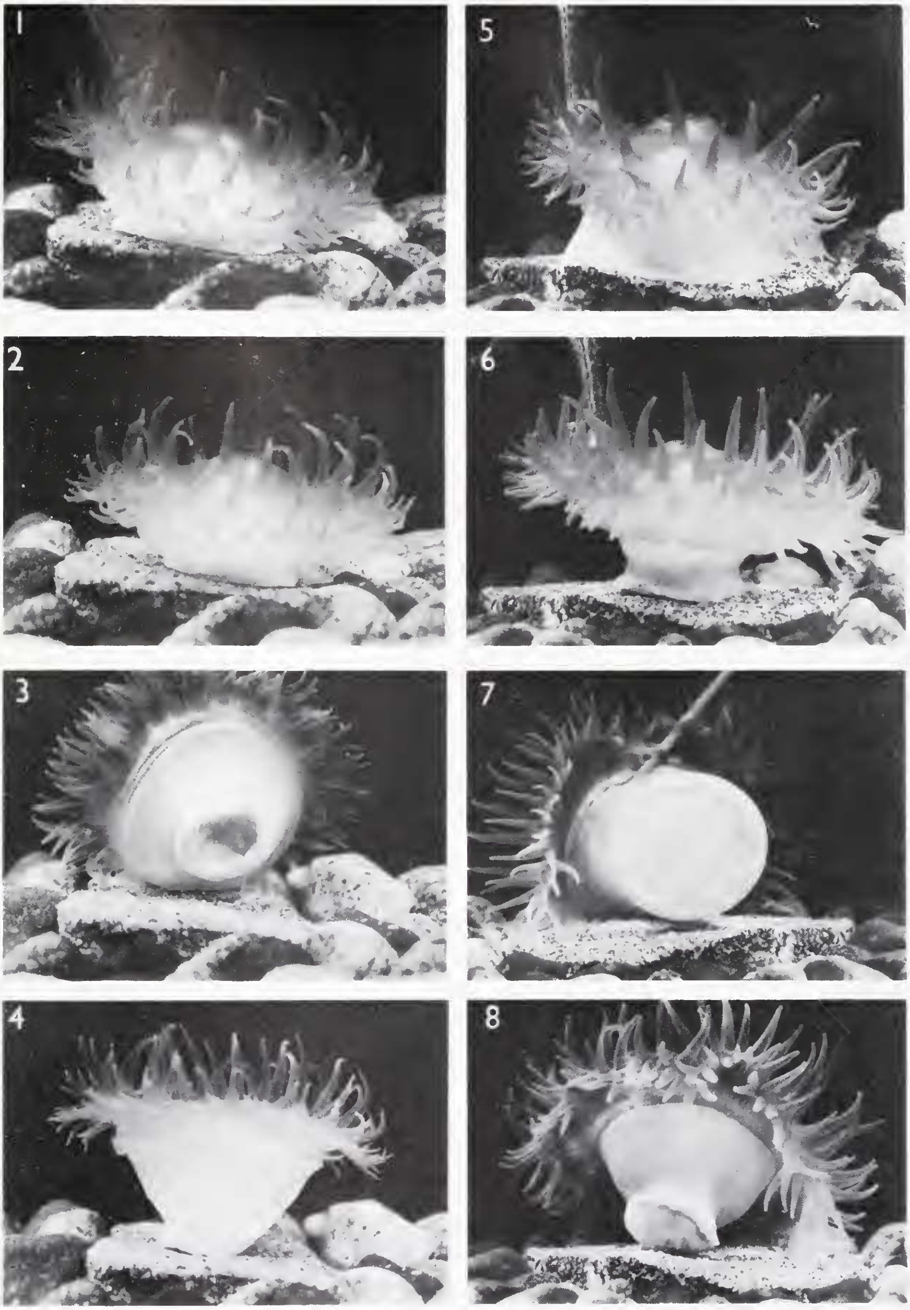
Unlike the responses of *Stomphia* spp. to *Dermasterias*, etc., the release of the pedal disk in *Tealia* sp. is not accompanied or followed by asymmetrical flexions ("swimming") or other repetitive activity. Resettlement often followed quickly, within 2–5 min, if the anemone remained upright. When the anemone fell over or was carried away by a current, resettlement did not begin until the pedal disk came against a surface to which it could adhere.

One of the 8 specimens of *Tealia* sp. was much larger than the others (pedal disk diameter 14 cm). This animal failed to release in response to *Dermasterias* on a number of occasions; in fact most of the trials which failed to cause release occurred with this animal. We found that the small and medium-sized specimens of *Tealia* sp. in our small collection gave more consistent and more rapid responses, and they were used more frequently in our tests. If a larger supply of animals could become available it would be interesting to see if a relationship exists between the size of the anemone and the frequency and speed of the release.

Figures 1–4 show a typical release of *Tealia* sp. when its tentacles were touched by *D. imbricata*. On a moderately extended specimen with the sea star touching the tentacles (Fig. 1) the diameter of the tentacular crown increased, the oral disk became convex, and the column shortened dramatically to about one-quarter of its original length (Fig. 2). These changes took place by slow, smooth movements, almost imperceptible as they happened but transforming the animal completely in less than half a minute.

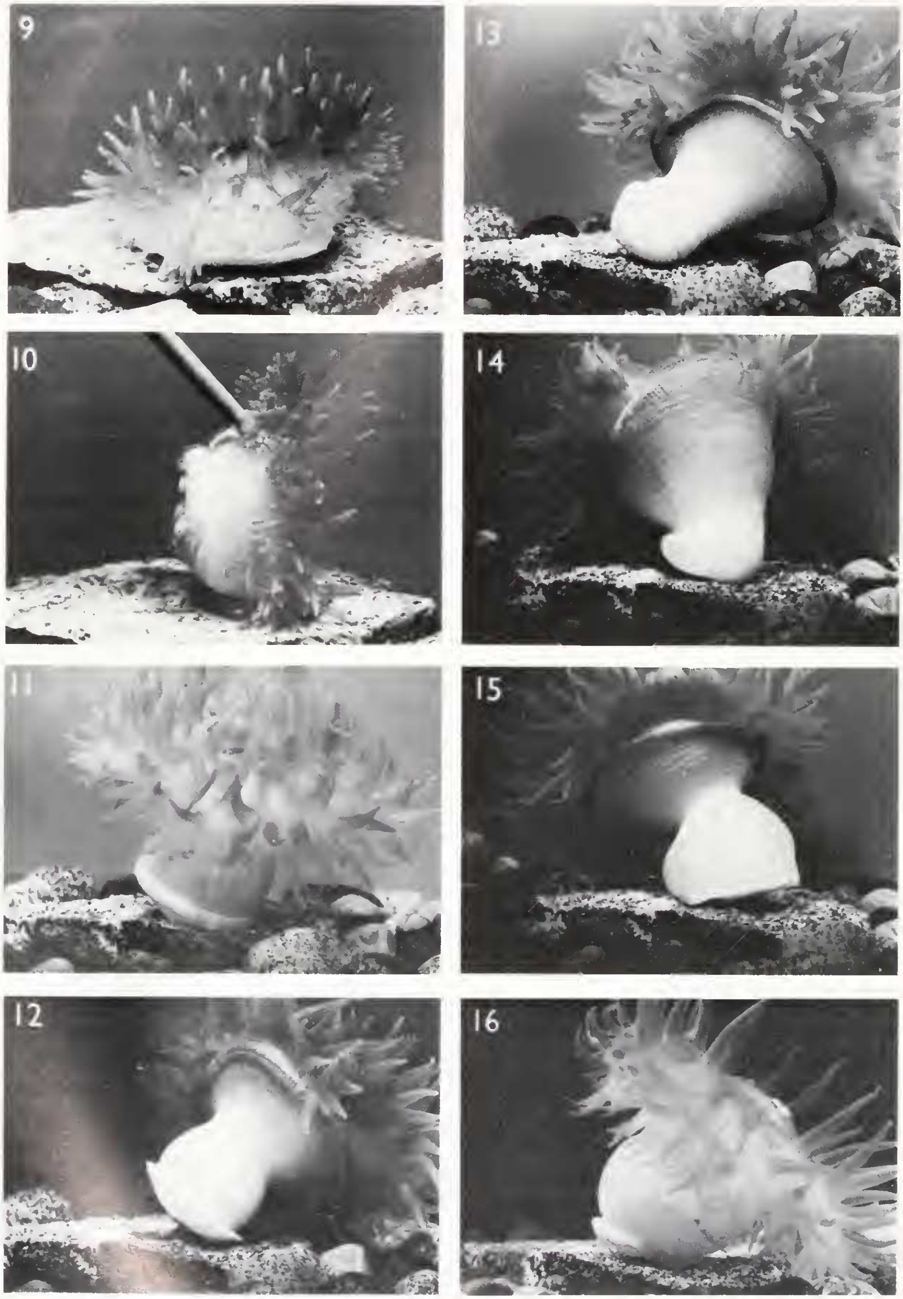
The shortening of the column was due in part to a constriction of the margin of the pedal disk to form a tightly contracted ring. Consequently the pedal disk no longer adhered and the anemone became detached and took on the shape of an inverted, almost medusoid, cone with the tentacular crown flared out and the pedal disk deeply concave (Fig. 3). Later, as the anemone began to resettle, about 3 min from the beginning, the column extended, and the constricted pedal disk began to adhere and extend outwards to bring the animal back to its normal position and appearance (Fig. 4).

Figures 5–8 show another example. This animal had a short column at the beginning (Fig. 5). About 15 sec after *Dermasterias* was brought in, the pedal disk lifted following the narrowing of the base (Fig. 6) and the flaring out of the crown and oral disk. Side views show the detached and almost flat pedal disk with a pattern of concentric grooves and at the center a slight elevation with a small central pit (Fig. 7). Later the base narrowed and resembled a terminal knob with the upper margin and crown still flared out and completely inactive, giving the animal the shape of a flower vase (Fig. 8). Then the pedal disk slowly assumed its normal dimensions and settlement proceeded as the disk spread across the stone. The entire response took less than 10 min.



FIGURES 1–8. *Tealia* sp. Two examples of pedal disk release and subsequent changes in shape in response to contact with *Dermasterias imbricata*. Full description in text. Time elapsed between Figures 1 and 4 approx. 2.5 min and between Figures 5 and 8 approx. 3.0 min.

There were minor variations around these patterns in the responses of our animals. Examples of some of the shapes assumed at various times are shown in Figures 9–16. It often happened also that an animal seemingly about to resettle



FIGURES 9–16. *Tealia* sp. Characteristic postures after release of pedal disk in response to *Dermasterias*. Note release and shortening of column (9, 10), swelling of pedal disk with upturned basal margin (11, 12, 13), extension of column with intermittent peristaltic waves (12, 14, 15, 16).

would fail to do so and would assume strange shapes and postures with strong peristaltic waves passing orally, before finally settling down.

The nudibranch, *Aeolidia papillosa*, which can cause *Stomphia* to detach and swim, induced detachment in *Tealia* sp. in three out of 11 trials. The release times

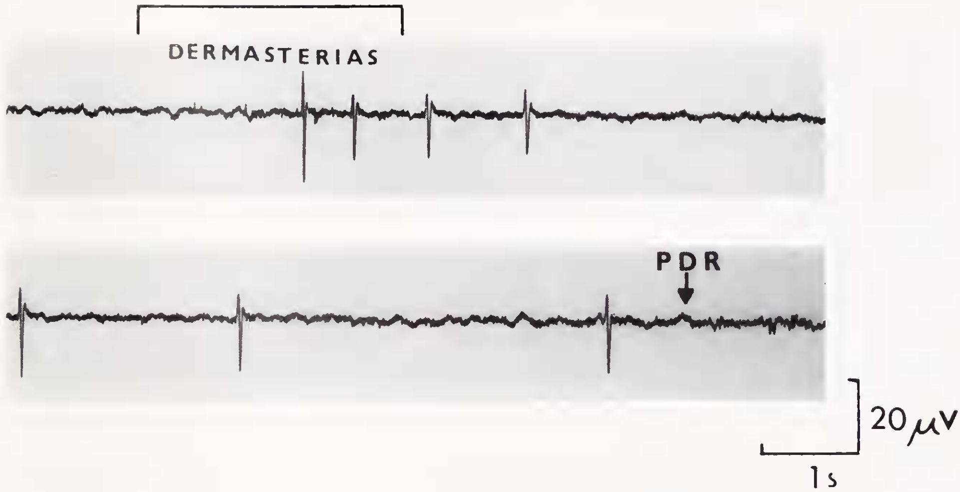


FIGURE 17. Electrical activity recorded from tentacles of *Tealia* sp. during and following 2.8 sec contact between *Dermasterias* and tentacles of anemone. Note 7 typical SS1 pulses. Arrow at PDR marks time of release of pedal disk. (Continuous trace; duration approx. 17 sec).

were long, 75, 80 and 240 sec. The responses differed from the response to the asteroids. Instead of spreading the oral disk outward, the anemone closed up and then released its pedal disk. It is interesting to note that *Hippasteria spinosa*, an asteroid that is highly successful in causing *Stomphia* to detach and swim, had no obvious effect on *Tealia* sp.

Electrophysiological data

McFarlane (1969a) and Lawn (1976) have described three types of pulses that have been recorded from sea anemones using standard electrophysiological techniques. These pulses are attributed to three different conduction systems that have become known by their initials: 1) NN (through-conducting nerve net located in the endoderm); 2) SS1 (slow system 1 located in the ectoderm); 3) SS2 (slow system 2 located in the endoderm). Each system has been linked to specific behavior patterns, *e.g.* NN with retraction and closure. SS1 pulses coincide with the release of the pedal disk in two cases: in *Calliactis parasitica* SS1 pulses accompany the slow release of the pedal disk in transfers to shells from other surfaces (McFarlane 1969b, 1973); in *Stomphia coccinea* SS1 pulses precede the release of the pedal disk in encounters with *Dermasterias* (Lawn, 1976). In a European *Tealia, T. felina* var. *lofotensis* (nomenclature of Stephenson, 1935), SS1 pulses triggered the prefeeding response that occurs when food substances come into contact with the column (McFarlane, 1970; Lawn, 1975). Thus there was reason to believe that SS1 pulses would be recorded in *Tealia* sp. and special interest attached to finding out whether SS1 pulses were associated also in this animal with the release of the pedal disk.

Figure 17 shows a typical record of the electrical activity in *Tealia* sp. when *Dermasterias imbricata* was brought up to the tentacles for a few seconds. Two SS1 pulses of characteristic appearance occurred about 2 sec after contact. Two more pulses followed at 1 sec intervals and three more followed with the intervals between pulses becoming longer until the anemone released its pedal disk, about 14 sec after the sea star made contact. This strongly suggests that the detachment of the pedal disk in *Tealia* sp. is triggered by a series of SS1 pulses.

The record shown in Figure 17 was preceded by a trace lasting several minutes from which SS1 pulses were conspicuously absent. Similar records were obtained, with pretrial controls, from three other specimens of *Tealia* sp. Further trials were carried out which gave similar records when the anemones had resettled. The relationship between SS1 pulses and the release of the pedal disk as seen in Figure 17 is not a statistical event; in our experience the two invariably occur together.

The SS1 pulses recorded before the detachment of *Tealia* sp. are almost identical with those that precede the detachment of the swimming anemone *Stomphia* (Lawn, 1976). The time that elapses between the application of the stimulus, the sea star, and the beginning of the response, is of the same order, usually a few seconds. The number of SS1 pulses preceding detachment is also of the same order in the two cases, usually from 6 to 12.

Examining records from a number of interactions between *D. imbricata* and *Tealia* sp. shows a good deal of variation in the number and the timing of pulses that trigger the release of the pedal disk on different occasions. A recurrent feature of the records was a tendency for two or three pulses to occur close together soon after contact was established between the two animals.

Pateria miniata, as reported earlier, sometimes evoked the releasing behavior, and it also set up trains of SS1 pulses. Of 10 trials, four resulted in detachment. The pulses in these records were similar to those in the interactions with *Dermasterias*, though generally the firing rate was lower, and in cases where release did not occur the pulses ceased after an initial two or three. Maintaining the activity after these first few pulses seems to be important to the triggering function.

Electrical stimulation of the SS1 in *Tealia* sp. caused detachment of the pedal disk and inflation of the oral disk. It was not possible to cut ectodermal flaps successfully in this anemone (McFarlane, 1969b), and this meant that the SS1 could not be stimulated separately from the nerve net. Results showed that the effective frequencies of stimulation fell in the range of one shock every 3 sec to one shock every 10 sec. The minimum number of shocks required to produce a response varied from four to eight depending on frequency. This corresponds closely to the situation previously encountered in *Stomphia* (Lawn, 1976).

Discussion

These results give rise to discussion on three topics: 1) comparative aspects; 2) the activity and mobility of the pedal disk; 3) the adaptational significance of the releasing behavior in *Tealia* sp.

Comparative aspects

Detachment in response to specific stimuli seems to be a general adaptation in a few genera in certain families. *Boloceroides*, in the family Boloceroididae, is a lightly attached Indo-Pacific anemone that releases quickly and swims actively in response to a nudibranch predator (Lawn and Ross, 1982). *Stomphia* spp. in the large family Actinostolidae, few of whose species have been observed alive, release quickly and "swim" in response to certain sea stars and nudibranchs (Robson, 1966; Ross, 1974). *Calliactis* spp., and other symbiotic actinians in the family Hormathiidae that live on crustaceans and gastropods, release their pedal disks slowly in response to shells or to the manipulations of certain hermit and spider crabs (Ross, 1974).

Tealia belongs to the Actiniidae, most of which are very firmly attached and difficult to dislodge, *e.g. Actinia* spp. This description applies to the familiar north-east Pacific species, *T. coriacea* and *T. crassicornis*. The fact that *Tealia* sp. and

T. piscivora can release quickly in interactions with certain animals in their environments, whereas four other species of *Tealia* cannot do so, shows that behavioral attributes often differ within taxa of generic or higher rank; within a genus or family these attributes may be restricted to particular species only. We see in this another example of the versatility of neuromuscular mechanisms in the actinians, often without any external signs of such special adaptations.

It is instructive to compare the behavioral physiology of *Tealia* sp. and *Stomphia* spp. in releasing the pedal disk. The SS1 conduction system is activated in both cases by the same stimulus, *Dermasterias*. The SS1 pulses trigger the release in similar ways; the number of pulses required, their frequency, and the latency of the response are of the same order of magnitude in both animals. However, the behavioral events that accompany and follow the release differ. In *Tealia* sp. the column shortens and the oral disk and tentacles flare out into an immense corona and contain most of the coelentric fluid. After this transformation, the anemone slowly returns to normal and resettles. The entire behavior proceeds without any movements except slow symmetrical changes of shape. Moreover, there is no evidence of the post-release or post-swimming torpor of *Stomphia* spp. Once *Tealia* sp. releases, the tentacles become extremely adhesive, unlike those of *Stomphia* which are non-adherent at this time. Whereas in *Tealia* sp., the column is greatly shortened during the release, in *Stomphia* it is greatly extended, and the release is accompanied and followed by swimming flexions for 2–3 min. Thus, almost identical triggering systems are used in the two cases to achieve different ends.

The pedal disk

These results reemphasize the sensory and motor activity taking place in the pedal disk in these special behavior patterns. Earlier examples were: the demonstration by Davenport *et al.* (1961) that the clinging of the tentacles of *Calliactis* on shells depended on information as to whether the pedal disk was on a shell or not; the description of the release and the resettlement of *Calliactis* and *Stomphia* showing the pedal disk to be an area in which many activities take place, *e.g.,* the symmetrical constriction bringing about release in *Calliactis* (Ross and Sutton, 1961); the swelling of the pedal disk to make contact with surfaces for settling in *Stomphia* and *Paracalliactis* (Ross, 1974); the description of the asymmetrical locomotory movements in *Metridium* (Batham and Pantin, 1950). The behavior of *Tealia* sp. described above provides another example of the activity of the pedal disk in actinian behavior, especially in anemones that abandon their sedentary habits from time to time.

Adaptational significance

The adaptational significance of the detachment behavior of *Tealia* sp. is far from clear. By analogy it looks like an escape response but there is no evidence that asteroids prey on *Tealia* sp. If it is an escape reaction, the anemone may employ it to escape from some other predator not yet discovered. Once detached, the expanded *Tealia* sp. is virtually weightless so that any current would carry it away and remove it from a potential predator. However, questions about the adaptational significance of the releasing behavior in *Tealia* sp. can only be answered with data from subtidal observations. Such studies are now in progress with *T. piscivora*. Unfortunately, *Tealia* sp. has been collected infrequently, its normal habitat is unknown, and it has not yet been located by divers, so we have no immediate prospect of observing it in nature.

Acknowledgments

The release of *Tealia piscivora* in response to an asteroid was first observed by Dr. W. Kokke, at the time our colleague in an investigation on the chemistry of *Dermasterias*. We acknowledge his contribution with pleasure and thank him for his continuing interest in this work. We also thank Miss Sandy Walde, a student at the University of Calgary, for assistance in the collection of behavioral and electrophysiological data. The support of Operating Grant No. A-1445 to D.M.R. from the Natural Sciences and Engineering Research Council of Canada is gratefully acknowledged.

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